ORIGINAL PAPER

Pollen production and circulation patterns along an elevation gradient in Mt Olympos (Greece) National Park

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Abstract We studied airborne pollen along an elevation gradient of Mt Olympos (Greece). Samples were collected on a regular basis, over the period March–October 2009, in eight elevation-different stations, by use of a portable Hirst-type volumetric sampler. Concurrently, we studied pollen production in *Quercus coccifera*, *Q. ilex*, *Pinus heldreichii* and *P. nigra*, which are dominant species in the main vegetation types of the mountain. Of the 35 pollen taxa detected in the air, 18 account for 99.1 % of the total airborne pollen. These are the main pollen taxa each contributing by at least 0.5 %. Pinaceae (32 %) followed by *Quercus* (24 %) and Urticaceae (18 %) are the most abundantly represented taxa. Duration of the pollen season decreases with elevation by on average 3 days for every 100 m of elevation increase or by 5 days for every Celsius-degree of temperature decrease. Pollen concentration in the air decreases with elevation for the lowland taxa; with the exception of Cupressaceae, no pattern is observed for the other main taxa. The pine and oak species studied carry comparable amounts of pollen, approximately 10^4 grains per flower, 10^8–10^9 per m^2 of crown surface and 10^{10}–10^{11} per individual; pollen production, primarily of the two *Quercus* species, is not responsive to environmental changes associated with elevation. Results provide evidence that, within a margin of error, airborne pollen reflects the distributions of pollen taxa on the mountain; regarding abundance, airborne pollen is representative of *Quercus*, but under-representative of Pinaceae. *Ambrosia* pollen is found at all elevations examined, although plants producing it have not been recorded on or around Mt Olympos.

Keywords Airborne pollen · Anemophilous trees · Flower production · *Pinus* · *Quercus* · Vegetation

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1 Introduction

Aerobiological research has developed in close relation to medical research. Responding to the needs of sensitized individuals and health agencies, networks of aerobiological stations have been established (Scheifinger et al. 2013) with continuous monitoring

of allergenic airborne pollen being their *raison d' être*. Assessment of data collected in these stations has allowed understanding of pollen circulation patterns (e.g. Rantio-Lehtimäki 1994) and prediction of pollen seasons (Van de Water et al. 2003; Sofiev et al. 2006). Given this primary use, it is not surprising that aerobiological data are drawn largely from stations located in or close to urban areas (Šikoparija et al. 2006; Rodríguez-Rajo et al. 2010) with very few addressing rural or natural environments. Nevertheless, pollen in the air is plants' fingerprint (Bryant 1990); it epitomizes plant phenological, reproductive and dispersal responses and reflects changes in biodiversity patterns. Monitoring pollen could contribute to answering important questions about the effect of various environmental factors, among which of global change (IPCC 2007), on organisms and communities. Obviously, studies addressing such issues cannot be confined in urban areas.

The European Union has taken many initiatives over the last decades to conserve the natural environment. The Natura-2000 network is a European Union wide network of nature protection areas aiming to assure the long-term survival of Europe's biodiversity (European Commission 2012). Climate change has been identified as a major factor threatening the survival of vulnerable species and habitats (Heller and Zavaleta 2009). We can respond to threats more efficiently if we have reliable estimates of the speed and magnitude of the changes that they induce on communities and species. Monitoring such changes is very important, especially in protected areas, which are established for the very reason of conserving valuable and vulnerable aspects of biodiversity.

Data from Europe and North America have shown that flowering of many anemophilous and entomophilous species has advanced earlier in the year. This is associated with temperature increase and holds true mainly for spring flowering species (Menzel et al. 2006; Levetin and Van de Water 2008; references therein). Apart from these widely documented phenological differences, the quantity of pollen is also shown to be affected by factors that are associated with global change presenting in several cases increasing trends (Rogers et al. 2006; Ziska et al. 2009). Given this, it is important to explore whether pollen production can become a reliable indicator of environmental variability.

Studies of pollen production along the elevation range of a species provide information on the plasticity of this character and on how varying environmental regimes influence reproductive characters. Studies of airborne pollen concentrations along such gradients enable understanding and forecasting pollen circulation patterns in the mountainous environment. Combining vegetation data with pollen data, we can examine how accurately the locally prevailing vegetation is reflected in the locally detected pollen. Despite their importance, there are only few flower and/or pollen production (Moe 1998; Blionis and Vokou 2001, 2002; Khanduri and Sharma 2002a, b) or pollen circulation (Gehrig and Peeters 2000; Tosunoglu et al. 2009; Jochner et al. 2012) studies along elevation gradients.

In the current work, we studied airborne pollen in Mt Olympos National Park. In elevation-different stations, we studied concurrently pollen production of four of the most abundantly represented woody anemophilous species in the mountainous vegetation. These species are two *Quercus* and two *Pinus* representatives, namely *Q. coccifera*, *Q. ilex*, *P. heldreichii* and *P. nigra*. The aim of our study was (1) to identify the locally prevailing airborne pollen patterns in terms of quantity, composition and temporal availability, (2) assess how responsive are the above four species to environmental variability associated with altitude, in terms of pollen production and (3) examine how well the airborne pollen reflects pollen taxa presence on the mountain.

Mt Olympos was selected for a number of reasons: (1) it is a Natura-2000 site and a national park; hence, there is adequate information on its vegetation, while results could be useful as background information for monitoring environmental change, (2) it is the highest mountain in Greece and unique in that it does not make part of a major range; it is an isolated mountain rising abruptly from close to the sea, and therefore, it makes a relatively simpler mountainous system, where to record and investigate airborne pollen patterns.

Apart from answering to questions regarding pollen production and atmospheric circulation along an elevation gradient, this work has also an applied aspect along the common line: for the first time, it provides necessary data for a local pollen calendar to serve the needs of pollen sensitized individuals, who are actual and potential visitors of one of the most visited national parks of the country.

2 Materials and methods

2.1 Study area

The study area, located at the north-central part of Greece (40°05′N, 22°21′E), is a site of the European Natura-2000 network (GR 1250001). It includes a large variety of habitat types and is rich in plant species. Almost 25 % of the country's flora is found there; fifty-six plant taxa are Greek endemics, of which 23 are local endemics. There are four main vegetation zones in the study area with *Pinus heldreichii* forming the timber (tree) line (Dafis et al. 1996; Strid 1980): (1) the evergreen-sclerophyllous (mediterranean shrub) vegetation (300–600 m), in which the selected species *Q. coccifera* and *Q. ilex* primarily occur, (2) the mixed beech and montane coniferous forests (700–1,500 m), in which *P. nigra* occurs, (3) the cool temperate coniferous forests (1,500–2,500 m), in which *P. heldreichii* dominates and (4) the alpine vegetation (2,500–2,917 m). The climate is mild to medium Mediterranean for areas in the range of 300–1,800 m and cold temperate above 1,800 m (Mavrommatis 1980).

2.2 Meteorological data

To have an estimate of the conditions prevailing in the study area, we used the existing data from four meteorological stations (at 900, 1,000, 1,150 and 1,600 m) for air temperature (°C), relative humidity (%), rainfall (mm), wind speed (km h^{-1}) and direction. For one station (1,600 m), the dataset was not complete: there were no rainfall data at all and no temperature data for August and September 2009.

2.3 Airborne pollen

Air samples were collected along the elevation gradient from 300 to 2,100 m, on a regular basis, every 10–15 days depending on weather conditions, over the period mid-March to early October 2009. In each sampling day, eight samples were collected, each lasting 30 min. Of these daily samples, three were taken at rest and five while in motion: two by car, at constant, low speed (30–35 km h^{-1}), and three on foot. The sampling design is illustrated in Fig. 1. Samples were also taken above 2,100 m, but we did not use them for the analysis, as they were very

incomplete; in several cases, sampling could not take place because of rain conditions at the high altitudes.

All samples were collected using a portable Hirst-type volumetric trap (Burkard Manufacturing, Hertfordshire, England), which operates under battery, at a nominal air throughput of 10 L min^{-1}. Sampling was conducted at approximately 1 m above ground level. Airborne pollen grains were directly collected onto glass slides coated with gelvatol; they were stained with a mixture of glycerol, gelatine, phenol and safranin and stored under cover slips. Pollen grains were counted and identified at 400× magnification using an optical microscope; they were expressed as mean daily pollen concentration per m^3 of air (Hirst 1952; British Aerobiology Federation 1995). Only data from taxa that contributed by at least 0.5 % to the total atmospheric pollen concentration over the entire
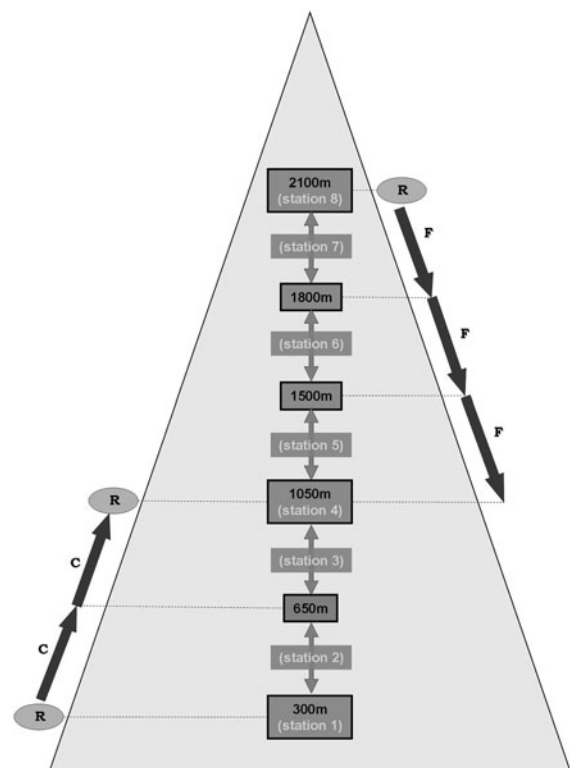

Fig. 1 Pollen sampling along the elevation gradient of Mt Olympos. Ovoid *shapes* indicate that the sample was taken while at rest (*R*) at a specific spot, and *arrows* that it was taken while in motion (*C* by car at low speed, *F* on foot); for the latter case, direction of *arrows* shows the sampling direction (while ascending or descending) while position and length of *arrows* shows the elevation range, at which sampling took place

period and elevation range were used for further analyses.

2.4 Pollen production

We estimated pollen production of the species *Pinus heldreichii*, *P. nigra*, *Quercus coccifera* and *Q. ilex*. Selection of these species was based on their being (1) among the most abundantly represented anemophilous species in the study area, (2) common species not only on Mt Olympos but in many other parts of the country and (3) members of the families of Fagaceae and Pinaceae that are widely represented globally. For each species, at least two stations that differ in elevation were selected (Table 1). Stations are representative of the species' distributions on the mountain and are located close to their low and high limits, from sites where species are locally abundant.

In each station (Table 1), we selected at random four healthy and mature individuals of the species under concern; we collected catkins for *Quercus* ssp. and strobili clusters for *Pinus* ssp., just before flowering, when stamens were not visible yet, from two opposite sides of their crowns. We counted the number of flowers contained in four catkins and four strobili as well as the number of strobili in four strobili clusters and measured length and maximum width of these reproductive structures as well as of *Quercus* flowers.

The floral unit that we used for the extraction of pollen for the two *Quercus* species was the flower, whereas for the two *Pinus* species, it was the strobilus.

In this study, *Pinus* microsporophylls and strobili are also referred to as flowers and inflorescences, respectively. Two floral units per selected individual were used, a total of 72 for all species and stations.

We took measurements of growth traits of the sampled individuals. In particular, we estimated (1) the height of crowns and individuals (in m) by use of the Blume-Leiss equipment (Matis 1994), (2) the crown diameter (in m), estimated as the average of two perpendicular to each other diameters of the crown at its widest part and (3) the trunk perimeter (in m); for *Q. coccifera*, which has the form of a shrub, the trunk perimeter was estimated as equal to the average perimeter of four main branches.

In order to estimate pollen production at levels higher than that of the floral unit sampled, we had to have a prior estimate of the production of floral units. In both *Quercus* and *Pinus* species, flowers/inflorescences appear mainly at the outer part of the crown, at the end of branches. In all selected individuals of each species, we counted the number of inflorescences (catkins for *Quercus* ssp.) or groups of inflorescences (strobili clusters for *Pinus* ssp.) within two sampling quadrats. The quadrat size differed depending on the density of floral units on the canopy of each species. It was 10 cm × 10 cm for *Q. coccifera*, 20 cm × 20 cm for *Q. ilex*, and 60 cm × 60 cm for *P. heldreichii* and *P. nigra* (Table 1).

To extract pollen grains, each floral unit was treated as suggested by Faegri and Iversen (1964), Moore et al. (1991) and Damialis et al. (2011), adjusted to the needs of the present study. In particular, each floral

Table 1 Sampling stations and sampling units for the estimation of pollen and flower production of two *Pinus* and two *Quercus* species

Taxon	Sampling station	Elevation (m)	Sampling unit	
			Pollen production	Flower production
P. heldreichii	Prionia	1,050 (Low)	Inflorescence	Strobili clusters in 0.60 m × 0.60 m of crown
	Refuge A′	1,800 (Medium)		
	Chondromessorachi	2,450 (High)		
P. nigra	Zilnia	650 (Low)	Inflorescence	Strobili clusters in 0.60 m × 0.60 m of crown
	Gortsia	950 (High)		
Q. coccifera	Litohoro	300 (Low)	Flower	Catkins in 0.10 m × 0.10 m of crown
	Zilnia	650 (High)		
Q. ilex	Litohoro	300 (Low)	Flower	Catkins in 0.20 m × 0.20 m of crown
	Zilnia	650 (High)		

unit was put into a 10 % KOH solution, crushed with a glass pole and boiled for 8 min; this allowed plant tissues to break up and release pollen grains. For *Q. coccifera* and *Q. ilex*, 65 % glycerol was added to a total volume of 0.5 mL in a 1 mL Eppendorf tube; for *P. heldreichii* and *P. nigra*, 80 % glycerol was added to a total volume of 10 mL. Using a CappAero micropipette (Capp A/S, Odense, Denmark), we took two samples (2 µL each) per suspension, while vigorously stirring it to ensure homogenisation and placed them on microscope slides under cover slips. Pollen grains on slides were counted with an optical microscope at 100× magnification.

Pollen production was estimated at different scales, taking into consideration the shape of floral units and crowns, as follows:

a. Estimation of the pollen content at the scale of the floral unit sampled

The number of pollen grains per floral unit, Pfu (flower for *Quercus*, inflorescence for *Pinus*; Table 1), was estimated after the equation:

$$P\text{fu} = \frac{V\text{su}}{V\text{sa}}\bar{p} \tag{1}$$

where Vsu and Vsa are the volumes of the suspension (in mL for *Pinus* and µL for *Quercus*) and of the sample taken (in µL), respectively, and $\bar{p}$ is the average over two replicates of the number of pollen grains in the sample.

b. Estimation of pollen production per flower or inflorescence

The number of *Pinus* pollen grains per flower Pfl and the number of *Quercus* pollen grains per inflorescence Pinfl were estimated after the following equations:

$$P\text{fl} = \frac{P\text{fu}}{fl} \tag{2a}$$

$$P\text{infl} = P\text{fu} \times fl \tag{2b}$$

where fl is the number of microsporophylls for *Pinus* and of flowers for *Quercus*.

The volume of floral units was estimated after the equation (Beyer 1984):

$$V = \frac{\pi \times d_1 \times d_2 \times d_3}{6} \tag{3}$$

where $\pi \approx 3.14$, d_1 and d_2 are two perpendicular diameters of the floral unit, at its widest part, and d_3 is

the floral unit's height. For *Pinus* strobili (spheroid shaped), $d_1 = d_2$ and for *Quercus* flowers (sphere shaped), $d_1 = d_2 = d_3$.

c. Estimation of pollen production at higher scales

The number of pollen grains per m^2 of crown Pcr was estimated after the equation:

$$P\text{cr} = P\text{fu} \times \frac{F\text{su}}{M} \tag{4}$$

where Pfu is the number of pollen grains per floral unit, as estimated above, Fsu is the average number of floral units per crown sampling unit (quadrat) and M is the area of the sampling unit.

The number of pollen grains per individual Pin was estimated after the equation:

$$P\text{in} = P\text{cr} \times S \tag{5}$$

where Pcr is the number of pollen grains per crown surface unit, as described above, and S is the total lateral surface area (in m^2) of the crown, estimated on the basis of the geometrical shape of the species' individuals. As the shapes of *Q. coccifera* and *Q. ilex* individuals approximate a spheroid and those of *P. nigra* and *P. heldreichii* a cone, the total lateral surface for the representatives of the two genera was estimated after the following equations (Beyer 1984):

1. for *Q. coccifera* and *Q. ilex*

$$S_Q = \frac{\pi \times d_m^2}{2} + \frac{2 \times \pi \times d_m \times h_c}{\frac{\sqrt{h_c^2 - d_m^2}}{h_c}} sin \frac{\sqrt{h_c^2 - d_m^2}}{h_c} \tag{6}$$

2. for *P. nigra* and *P. heldreichii*

$$S_P = \frac{\pi \times d_m}{2} \sqrt{\frac{d_m^2}{4} + h_c^2} \tag{7}$$

where $\pi \approx 3.14$, d_m is the average crown diameter and h_c is the crown height.

2.5 *Quercus* and Pinaceae representation in the study area

To have an estimate of Pinaceae and *Quercus* presence on the mountain, we made use of the maps of the Corine Land Cover (CLC) for Greece, for the area of Mt Olympos. The distribution of the different

Fig. 2 Map of the mountain with the different Corine Land Cover (CLC) types. Shown are Mt Olympos National Park boundary and also the aspect of the mountain (pollen catchment area) within which we took all our samples
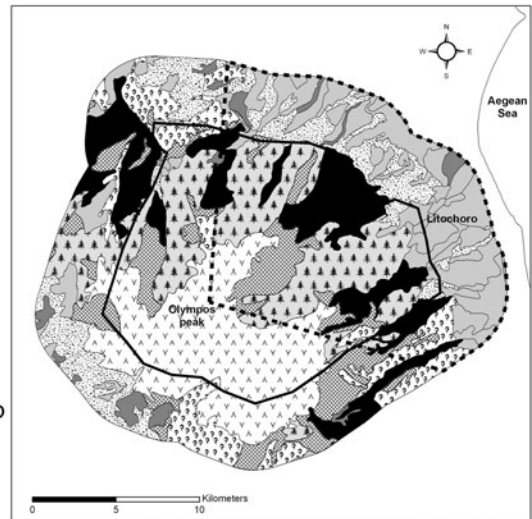
CLC types on the mountain is shown in Fig. 2. We used vegetation data for the area (YPEHODE 1999–2001) in order to estimate the average cover of species belonging to these two taxa in each CLC type. The total surface of the mountain, delineated in Fig. 2, and the surface of each CLC type were estimated using ArcGIS. Based on these, we estimated the surface covered on the mountain by each species belonging to Pinaceae and *Quercus*. To do this, we used existing vegetation data, specifically the species' covers that had been recorded in vegetation plots sampled in the area (YPEHODE 1999–2001); the shrub and tree layers were used for the calculations. Average species covers per CLC type were estimated on the basis of the vegetation plots sampled in the habitat types corresponding to the specific CLC type. As species cover data in the database are at the Braun-Blanquet ordinal scale, they were transformed to quantitative cover data after the default correspondence used in TURBOVEG ver. 2.84 (Hennekens and Schaminée 2001).

To examine how well Pinaceae and *Quercus* contribution in the local vegetation is reflected in the airborne pollen, we used a ratio commonly estimated in soil palynological studies (Heim 1970): the pollen-vegetation ratio $R = P/V$, where P is the per cent contribution of pollen of the specific taxon to the total airborne pollen, and V is the per cent cover of the

specific taxon to the total surface of the area under concern. For values close to 1, taxa are well represented, and for values well above 1, taxa are over-represented, whereas for values well below 1, they are under-represented in the airborne pollen of the area.

2.6 Statistical analysis

a. Meteorological data

We checked for differences among meteorological stations in temperature, rainfall, relative humidity and wind speed with analysis of variance (ANOVA) and post hoc tests (Bonferroni) only for the days that sampling of airborne pollen took place. We also analysed blowing winds and estimated the frequency and speed at which winds of different direction blew during the days of sampling.

b. Airborne pollen

To estimate the temporal and quantitative features of pollen seasons, we used linear interpolation; we carried out interpolation separately per taxon and station. We define the start and end of the pollen season as the date corresponding to 2.5 and 97.5 %, respectively, of the taxon's pollen grains over the entire period (Andersen 1991). To estimate the contribution of each pollen taxon to the airborne pollen of the mountain overall, we estimated per-day

averages across stations that are expressed as number of grains per m^3 of air and summed these daily averages over the whole season.

For every taxon, counts vary largely over the sampling period, from zero, when pollen is absent, to very high, when pollen is locally abundant. Given the high participation of zero values in our data representing absence of pollen, at one or more stations, at one or more sampling times, we could not apply statistically appropriate methods for transforming them. Hence, we could not submit data to regular analyses of variance or covariance. To examine whether the representation of pollen taxa in the airborne pollen differs depending on their elevation distribution, we estimated per-station average counts across sampling days for each taxon and further submitted these average values to regression analysis with elevation.

c. Pollen production

We checked for differences among species, genera and sampling stations after elevation with analysis of variance (ANOVA) and post hoc tests (Bonferroni). The estimated numbers of pollen grains and flowers at different scales (up to the level of crown surface unit) were assessed separately for each species by analysis of covariance (ANCOVA); elevation was the categorical predictor, whereas the size of the reproductive and growth traits studied were the covariates. Second-degree factorial analysis was used for the detection of differences due to these factors.

All statistical analyses were carried out in Statistica 7.

3 Results

3.1 Meteorological factors

Air temperature, rainfall, wind speed and relative humidity values in 2009 from four meteorological stations on Mt Olympos are presented in Fig. 3a–d, respectively. Statistical analyses for these parameters, but only for the days at which sampling took place, showed that temperature was considerably lower at the highest station (1,600 m) and that relative humidity decreased with elevation (Table 2). As sampling took place on rather rainless days, average rainfall values were low and not differing among stations. Wind speed did not differ between the two lower or the two upper stations, but there was a considerable difference between the two groups (Table 2). Winds blew more frequently from N, W, NW and NE direction and were mild on all sampling days (Table 3).

3.2 Pollen taxa representation in the airborne pollen

Thirty-five taxa are represented in the airborne pollen of the study area. Of these, only 18 (Table 4)

Fig. 3 Meteorological data from four stations on Mt Olympos, at 900, 1,000, 1,150 and 1,600 m, for 2009; **a** air temperature in °C (average ± standard deviation), **b** rainfall in mm, **c** wind speed in m sec^{-1} (average ± standard deviation) and **d** relative humidity as per cent (average ± standard deviation)
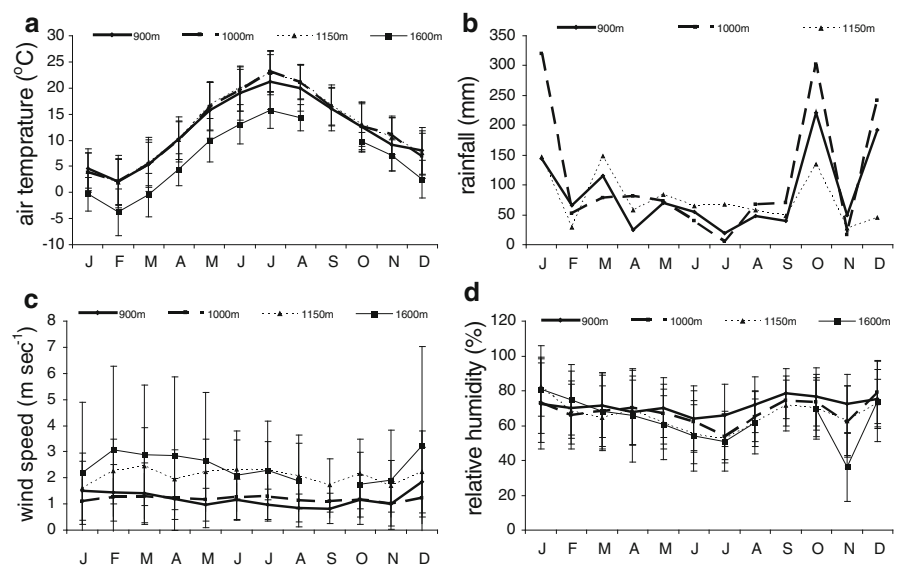
Table 2 Average values (±standard deviation) of meteorological parameters from four stations on Mt Olympos for the days that sampling of airborne pollen took place

Stations	Air temperature (°C)	Rainfall (mm)	Relative humidity (%)	Wind speed (m sec^{-1})
900 m	17.8 (±6.56)[c]	0.07 (±0.47)[a]	68.6 (±18.05)[a]	1.0 (±0.69)[b]
1,000 m	18.9 (±6.09)[a,b]	0.06 (±0.46)[a]	62.3 (±16.86)[b]	1.2 (±0.49)[b]
1,150 m	19.1 (±6.15)[a]	0.04 (±0.29)[a]	58.1 (±15.79)[c]	2.2 (±1.13)[a]
1,600 m	13.0 (±6.04)[d]	–	54.7 (±19.68)[c]	2.3 (±2.01)[a]

Letters "a–d" show significant differences ($p < 0.05$) of the parameters examined among stations; "a" corresponds to highest and "d" to lowest values

Table 3 Direction, speed (average ± standard deviation) and frequency of blowing winds for the days that sampling took place; data from four meteorological stations (see Table 2)

Wind direction	Frequency (%)	Average wind speed (km h^{-1})
N	21.0	5.9 (±5.6)
NE	12.3	6.6 (±5.6)
NW	16.0	3.9 (±3.2)
S	7.4	5.8 (±6.4)
SE	8.6	4.5 (±2.3)
SW	7.4	6.0 (±3.6)
E	9.9	6.3 (±4.4)
W	17.3	5.9 (±3.8)

contribute by at least 0.5 % accounting for 99.1 % of the airborne pollen over the entire period and elevation range. We define these as main pollen taxa. Pinaceae, *Quercus* and Urticaceae are the taxa with the highest contribution; they make more than 70 % of the airborne pollen in the area. The other pollen types that were detected but had only a minor contribution are *Acer*, *Alnus*, *Betula*, *Carpinus*, Cichorioideae, Cyperaceae, Ericaceae, *Fagus*, *Juglans*, Myrtaceae, Papaveraceae, *Populus*, Rosaceae, *Rumex*, *Tilia*, *Tsuga*, Typhaceae. Of the 18 main pollen taxa, 10 have herbaceous and eight woody representatives; in their majority, they are strictly anemophilous taxa (i.e. Pinaceae, *Quercus*), but ambophilous (i.e. *Plantago*, Chenopodiaceae/Amaranthaceae) and entomophilous taxa [Asteroideae, Apiaceae (Table 4)] were also recorded.

Maximum daily pollen concentrations were recorded at low-elevation stations (below 1,500 m) for 15 of the 18 main pollen taxa (Table 4). Among the most abundantly represented taxa, six correspond to purely or mainly lowland taxa (*Olea*, *Platanus*, other

Oleaceae, *Quercus*, Chenopodiaceae/Amaranthaceae, *Salix*) (Strid 1980). Except for other Oleaceae, for these taxa, pollen concentration and elevation are inversely related (Fig. 4). Regarding *Ambrosia* that has not been detected on and around Mt Olympos, no elevation pattern for its airborne pollen was observed. None of the remaining 11 main pollen taxa is of only upland distribution, so we could not examine if the pattern gets inversed; they are mostly of wide altitudinal distribution. No elevation pattern was detected for them with the exception of Cupressaceae; their pollen concentration decreases steeply with elevation. This must be related to the considerable pollen input from cypress trees that are planted in the area of Litochoro, at the foot of the mountain.

3.3 Pollen-season patterns

Pollen season starts with different taxa at the different stations, but ends everywhere with *Ambrosia*. At the mountain scale, the longest pollen seasons correspond to Asteroideae, Poaceae and *Plantago*, whereas the shortest to *Ambrosia* and Cannabaceae. From early May to late August, pollen grains from more than 10 main pollen taxa are concurrently present in the air (Fig. 5). Pollen seasons in Fig. 5a were calculated after all sampling days and all different stations, whereas in Fig. 5b–d, they correspond to the stations at 300 m (Litochoro), 1,050 m (Prionia) and 2,100 m (Refuge A') respectively. As sampling on the mountain started in March, it is possible that we underestimated the duration of pollen seasons for winter-flowering taxa (e.g. *Corylus*, Cupressaceae, *Fagus*) and also the total pollen that they contribute.

There are pronounced changes of pollen-season attributes with elevation. At 2,100 m, the start delays by about 2 months compared to that at 300 m (mid-May and mid-March, respectively). For the majority

Table 4 Pollen taxa participating with more than 0.5 % to the total airborne pollen of Mt Olympos (Greece), per cent contribution, maximum daily concentrations and annual sums, as estimated after linear interpolation, over the period March–October 2009; growth form and pollination mode are also given for each taxon

Taxon	Growth form[a]	Pollination mode[b]	Annual sum (grains m^{-3} air)	Contribution to the total pollen concentration (%)	Maximum daily concentration; the respective sampling station in parenthesis (grains m^{-3} air)
Pinaceae	WE	A	9,877	31.5	283 (300 m)
Quercus spp.	WE	A	7,458	23.8	149 (301–650 m)
Urticaceae	H	A	5,666	18.1	271 (2,100 m)
Cupressaceae	WE	A	2,054	6.5	38 (301–650 m)
Poaceae	H	A,S	1,568	5.0	20 (300 m)
Plantago spp.	H	A,E	666	2.1	8 (300 m)
Platanus spp.	WD	A	662	2.1	15 (300 m)
Ambrosia spp.	H	A	436	1.4	25 (300 m)
Castanea spp.	WD	A	432	1.4	23 (300 m)
Olea spp.	WE	A,E	392	1.3	9 (300 m)
Chenopodiaceae[c]	H	A,E	351	1.1	10 (1,050 m)
Salix spp.	WE,WD	A,E	321	1.0	7 (301–650 m)
Other Oleaceae	WE	A,E	308	1.0	6 (300 m)
Artemisia spp.	H	A	216	0.7	7 (301–650 m)
Apiaceae	H	E	186	0.6	5 (2,100 m)
Other Asteroideae	H	E	170	0.5	5 (1,050 m)
Cannabaceae	H	A	157	0.5	5 (1,050 m)
Thalictrum spp.	H	A	153	0.5	3 (2,100 m)
Other taxa			283	<0.5 %	<2
Total			31,356	100	3,942

Taxa are ordered after their contribution to the total pollen load. WE, WD, and H correspond to woody evergreen, woody deciduous, and (primarily) herbaceous plants, respectively, whereas A, E and S correspond to anemophilous, entomophilous and self-pollinated taxa, respectively

[a] After Tutin et al. (1968–1980, 1993), Lewis et al. (1983)

[b] After Lewis et al. (1983)

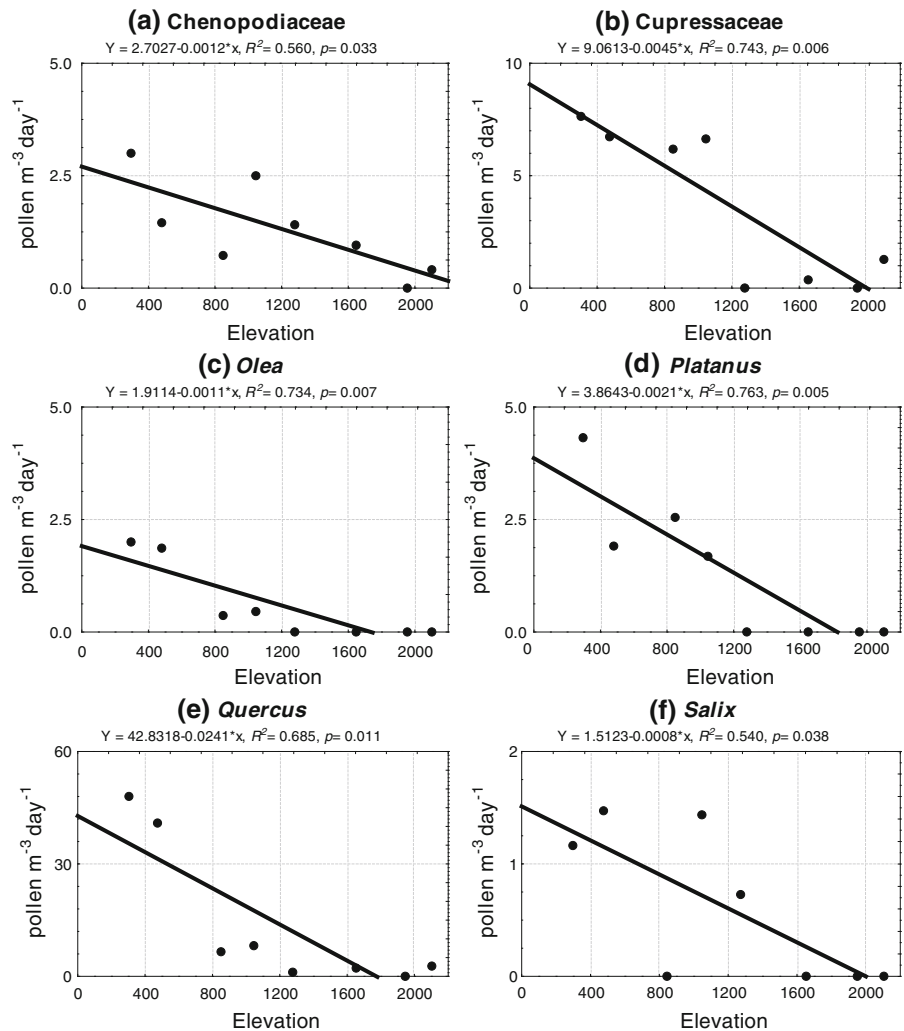[c] Amaranthaceae are also included in this taxon

of taxa, delays in the start result into shortening of the pollen-season duration as the mountainous conditions are prohibitive to similar shifts of the end later in the year; shortening becomes dramatic for some taxa like Asteroideae and Poaceae, for which the 6-month period at 300 m (Fig. 5b) becomes 3 month at 2100 (Fig. 5d). The average duration of the pollen season for the 18 main taxa decreases by approximately 3 days for every 100 m of elevation increase (Fig. 6a). Taking into consideration the standard adiabatic lapse rate at the latitude of Mt Olympos, which is 0.6 °C per 100 m (Smith et al. 2006), we estimated a 5-day decrease in the average pollen season for one Celsius-degree decrease in temperature. The rank of species appearing first in the air changes with elevation (Fig. 5) and so does the number of main pollen taxa (Fig. 6b); for every 1,000 m of elevation increase, the number of main pollen taxa drops by approximately four.

3.4 Pollen production

Pollen production of the four woody taxa studied is of similar magnitude; it is approximately 10^4 per flower, 10^8–10^9 per m^2 of crown surface and 10^{10}–10^{11} per individual (Table 5). Nonetheless, *Q. coccifera* produces significantly more pollen per flower, whereas *Pinus* species produce more pollen per inflorescence

Fig. 4 Main pollen taxa (participating with more than 0.5 % to the total airborne pollen of the mountain overall) that present significant trends of change of pollen concentration in the air with elevation. Given are the average pollen counts over the entire season per sampling station, the regression equations between these counts and elevation, R^2, and the corresponding p values

(a) Chenopodiaceae
$Y = 2.7027-0.0012*x$, $R^2 = 0.560$, $p = 0.033$

(b) Cupressaceae
$Y = 9.0613-0.0045*x$, $R^2 = 0.743$, $p = 0.006$

(c) *Olea*
$Y = 1.9114-0.0011*x$, $R^2 = 0.734$, $p = 0.007$

(d) *Platanus*
$Y = 3.8643-0.0021*x$, $R^2 = 0.763$, $p = 0.005$

(e) *Quercus*
$Y = 42.8318-0.0241*x$, $R^2 = 0.685$, $p = 0.011$

(f) *Salix*
$Y = 1.5123-0.0008*x$, $R^2 = 0.540$, $p = 0.038$

than the other species. Within *Pinus*, *P. heldreichii* produces a higher number of strobili per strobili cluster than *P. nigra*, but the latter produces higher numbers of microsporophylls per strobilus; as a consequence, the two species have similar microsporophyll and pollen production per strobili cluster.

Elevation-specific results regarding the reproductive output of the four species are given in Table 6. Significant elevation differences were observed only for *Pinus* species. More specifically, *P. nigra* produces more pollen per flower (microsporophyll) at the high station (950 m), whereas *P. heldreichii* produces fewer flowers (microsporophylls) per inflorescence (strobili) at the two high stations (1,850, 2,450 m).

The size of reproductive structures (flowers, inflorescences, strobili clusters) and growth attributes of the individuals sampled are given in Table 7. ANCOVA revealed significant effects ($p < 0.05$) of the floral unit size on the production of microsporophylls and pollen in *Pinus* species, but no effect was observed in *Quercus*. The reproductive output per crown surface unit was not influenced by the growth attributes of the individuals sampled for *P. heldreichii* and *Q. coccifera*; trunk perimeter had an effect only on the number of pollen grains in *P. nigra*, whereas plant height influenced the number of flowers and inflorescences in *P. nigra* and *Q. ilex* ($p < 0.05$).
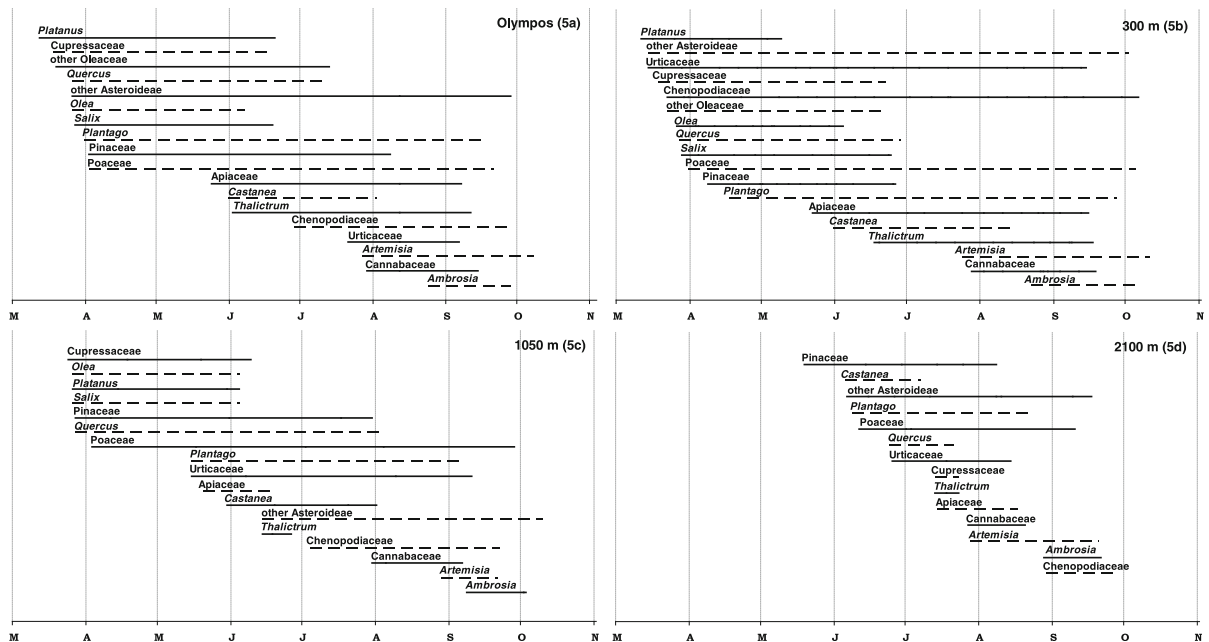
Fig. 5 Pollen seasons of the 18 main pollen taxa (participating with more than 0.5 % to the total airborne pollen of the mountain overall), during the period March–October 2009, **a** for Mt Olympos, on the basis of the eight stations covering the range 300–2,100 m, **b** at 300 m, in the town of Litochoro, at the foot of the mountain, **c** at 1,050 m, at Prionia site and **d** at 2,100 m, close to the mountain Refuge A
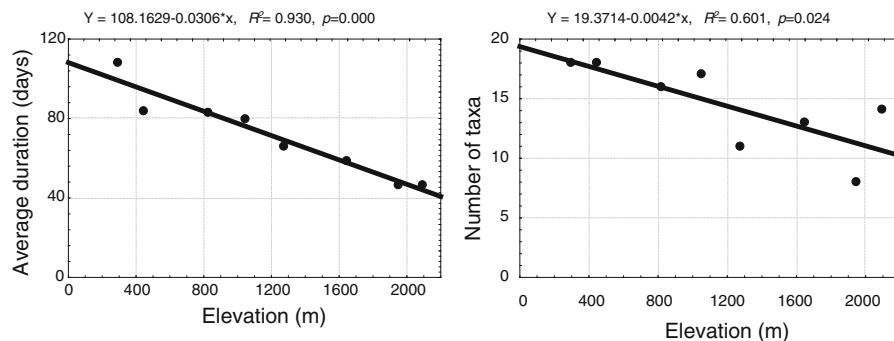

Fig. 6 Relationships between **a** the duration of the pollen season and **b** the number of main pollen taxa with elevation; values for each elevation are the averages of pollen-season durations for all species present there. Given are the regression equations, R^2, and the corresponding p values

3.5 *Quercus* and Pinaceae representation in vegetation and airborne pollen

The surface covered by species belonging to *Quercus* and Pinaceae that occur on Mt Olympos are given in Table 8. We estimated the size of surfaces covered by each participating species of these two pollen taxa on the basis of the total area of the mountain delineated in Fig. 2 and of the different CLC types, where it participates; we also estimated respective surfaces for

a fraction of the mountainous area corresponding to the aspect, wherefrom we took our samples, which we define as pollen catchment area. The pollen concentration ratio of Pinaceae and *Quercus* (1.32) differs from the ratio of the surfaces that they cover (1.69 for the mountain, 2.79 for the pollen catchment area). They both show Pinaceae dominance, but not as high in pollen as in surface. Regarding the pollen-vegetation ratio (*P/V*), it is around 1 for *Quercus*, but well below 1 for Pinaceae; these values correspond to fair

Table 5 Average flower and pollen production (±standard deviation) of two *Quercus* and two *Pinus* species at different scales over all stations sampled

Taxon	Flower production*						Pollen production				
	Flowers per inflorescence	Flowers per strobili cluster	Flowers per m² crown surface	Strobili per strobili cluster	Inflorescences per m² crown surface	Strobili clusters per m² crown surface	Pollen grains per flower	Pollen grains per inflorescence	Pollen grains per strobili cluster	Pollen grains per m² crown surface	Pollen grains per individual
P. heldreichii	131.9 (±33.7)[b]	3.2×10^3 (±1.4×10^3)[a]	4.4×10^4 (±2.2×10^4)[ab]	23.6 (±6.9)[a]	5.4×10^2 (±1.9×10^2)[b]	22.0 (±5.5)[b]	8.7×10^3 (±3.4×10^3)[b]	1.2×10^6 (±0.7×10^6)[b]	2.9×10^7 (±2.1×10^7)[a]	7.0×10^8 (±5.6×10^8)[bc]	2.3×10^{10} (±3.3×10^{10})[a]
P. nigra	223.6 (±50.2)[a]	2.5×10^3 (±1.4×10^3)[a]	8.3×10^4 (±7.9×10^4)[a]	11.1 (±8.7)[b]	5.9×10^2 (±5.5×10^2)[b]	49.7 (±22.4)[a]	7.8×10^3 (±2.8×10^3)[b]	1.8×10^6 (±0.9×10^6)[b]	1.9×10^7 (±1.0×10^7)[a]	1.0×10^9 (±0.8×10^9)[ab]	1.4×10^{11} (±1.3×10^{11})[a]
Q. coccifera	14.7 (±1.8)[c]	–	1.0×10^5 (±0.4×10^5)[a]	–	6.9×10^3 (±2.1×10^3)[a]	–	1.5×10^4 (±0.7×10^4)[a]	2.2×10^5 (±1.0×10^5)[c]	–	1.6×10^9 (±0.8×10^9)[a]	1.6×10^{11} (±1.7×10^{11})[a]
Q. ilex	18.9 (±4.4)[c]	–	1.4×10^4 (±0.9×10^4)[b]	–	7.5×10^2 (±4.7×10^2)[b]	–	9.0×10^3 (±7.1×10^3)[b]	1.8×10^5 (±1.6×10^5)[c]	–	1.4×10^8 (±1.2×10^8)[c]	2.1×10^{11} (±2.5×10^{11})[a]

Letters "a–c" show significant differences ($p < 0.05$) of the parameters examined among species; "a" corresponds to the highest and "c" to the lowest values

* In *Pinus* spp., flowers and inflorescences correspond to microsporophylls and strobili, respectively

representation for *Quercus*, but under-representation for Pinaceae.

4 Discussion

Pinaceae, *Quercus*, Urticaceae and Cupressaceae are the four most abundantly represented taxa in the air of Mt Olympos. The same taxa are the most abundant also in the urban environment of Thessaloniki (Damialis et al. 2007), approximately 75 km away. Pollen from Urticaceae species, although they are favoured in disturbed habitats, is relatively more abundant in the study area (18.1 %) than in Thessaloniki (10.8 %). Woody taxa contribute more to the airborne pollen of Mt Olympos (69.6 %) than herbaceaous taxa; the same holds true for Thessaloniki (75.8 %). In fact, this is also observed in areas from the south, mid- and north Europe, that is, from areas with different climate and vegetation, as Italy [55 % (Romano et al. 1988)], Finland [82 % (Koivikko et al. 1986)], Poland [73 % (Kasprzyk 1996)], Switzerland [>70 % (Clot 2003)], Turkey [64.1–94.0 % (Erkan et al. 2011; references therein].

Pollen dispersal and transport into mountainous areas, where steep slopes prevail, can be intricate and unpredictable and the levels of atmospheric pollen concentrations can increase or decrease depending on how the mountain acts, that is, as a source or as an obstacle for pollen transport. Environmental factors contributing to this high variability in the mountainous environment are air temperature, precipitation, relative humidity and wind speed and direction (Bush 1989) that vary considerably along the elevation gradient. Alternate wind circulation phenomena during day and night (Flokas 1994) can provoke movement and further mixing of air masses and, consequently, also of pollen (McDonald 1979, 1980). Despite these, there were steep decreases with elevation in the atmospheric concentration of pollen from lowland taxa suggesting a rather limited mixing of pollen along the elevation gradient, at least within the range of meteorological conditions that prevailed during our samplings.

One of the few publications that examine airborne pollen concentrations at different altitudes showed pollen decrease for some taxa (e.g. for *Alnus glutinosa*) or increase for some others (e.g. *Alnus viridis*) at high altitudes (Jochner et al. 2012). For grasses, we did

Table 6 Flower and pollen production (mean ± standard deviation) of two *Pinus* and two *Quercus* species at different scales, from sampling stations differing in elevation

Taxon	Sampling station (m)	Flower production*			Pollen production			
		Flowers per inflorescence	Flowers per m^2 crown surface	Inflorescences per m^2 crown surface	Per flower	Per inflorescence	Per m^2 crown surface	Per individual
P. heldreichii	1,050	152.1 (±19.0)[a]	4.6×10^4 (±2.8×10^4)[ab]	20.1 (±6.2)[a]	1.0×10^4 (±0.4×10^4)[a]	1.5×10^6 (±0.5×10^6)[a]	7.5×10^8 (±5.2×10^8)[ab]	5.2×10^{10} (±4.7×10^{10})[a]
	1,800	149.1 (±25.4)[a]	5.7×10^4 (±3.2×10^4)[a]	25.7 (±7.7)[a]	1.0×10^4 (±0.3×10^4)[a]	1.6×10^6 (±0.6×10^6)[a]	1.0×10^9 (±0.8×10^9)[a]	1.5×10^{10} (±1.0×10^{10})[b]
	2,450	94.4 (±14.9)[b]	3.0×10^4 (±1.6×10^4)[b]	20.1 (±5.7)[a]	5.8×10^3 (±1.8×10^3)[b]	5.4×10^5 (±1.7×10^5)[b]	2.9×10^8 (±1.6×10^8)[b]	3.9×10^9 (±1.5×10^9)[b]
P. nigra	650	243.5 (±64.9)[a]	6.4×10^4 (±3.4×10^4)[a]	46.8 (±12.8)[a]	7.1×10^3 (±3.0×10^3)[a]	1.6×10^7 (±1.0×10^7)[a]	8.4×10^8 (±5.9×10^8)[a]	1.1×10^{11} (±1.2×10^{11})[a]
	950	208.6 (±26.9)[a]	1.0×10^5 (±1.1×10^5)[a]	53.8 (±33.9)[a]	8.4×10^3 (±2.7×10^3)[a]	2.1×10^7 (±0.9×10^7)[a]	1.2×10^9 (±0.9×10^9)[a]	1.8×10^{11} (±1.5×10^{11})[a]
Q. coccifera	300	18.3 (±3.8)[a]	1.7×10^4 (±1.0×10^4)[a]	0.9×10^3 (±0.5×10^3)[a]	1.1×10^4 (±0.9×10^4)[a]	2.2×10^5 (±1.9×10^5)[a]	1.9×10^8 (±1.5×10^8)[a]	2.1×10^{11} (±2.1×10^{11})[a]
	650	19.7 (±4.9)[a]	1.1×10^4 (±0.7×10^4)[a]	0.6×10^3 (±0.4×10^3)[a]	7.2×10^3 (±4.3×10^3)[a]	1.5×10^5 (±0.9×10^5)[a]	0.9×10^8 (±1.0×10^8)[a]	9.4×10^{10} (±6.6×10^{10})[a]
Q. ilex	300	14.2 (±1.9)[a]	9.8×10^4 (±4.5×10^4)[a]	6.7×10^3 (±2.4×10^3)[a]	1.8×10^4 (±0.8×10^4)[a]	2.6×10^5 (±1.2×10^5)[a]	1.8×10^9 (±1.3×10^9)[a]	3.8×10^{11} (±2.5×10^{11})[a]
	650	15.3 (±1.5)[a]	1.1×10^5 (±0.4×10^5)[a]	7.1×10^3 (±2.8×10^3)[a]	1.2×10^4 (±0.2×10^4)[a]	1.8×10^5 (±0.3×10^5)[b]	1.3×10^9 (±0.6×10^9)[b]	3.5×10^{10} (±2.6×10^{10})[b]

Letters "a–b" show significant differences ($p < 0.05$) of the parameters examined among stations of the same species; "a" corresponds to the highest and "b" to the lowest values

* In *Pinus* spp., flowers and inflorescences correspond to microsporophylls and strobili, respectively

Table 7 Size of floral units (volume) and of growth attributes (trunk perimeter, plant height, crown surface) (mean ± standard deviation) of two *Pinus* and two *Quercus* species from sampling stations differing in elevation

Taxon	Sampling station elevation (m)	Size of floral units (mm^3)			Size of growth attributes		
		Flower*	Inflorescence*	Strobili cluster	Trunk perimeter (m)	Height (m)	Crown surface (m^2)
P. heldreichii	1,050	3.3	4.3×10^2	1.6×10^4	0.7	4.5	67.5
		$(\pm 0.6)^a$	$(\pm 1.4 \times 10^2)^a$	$(\pm 0.6 \times 10^4)^{ab}$	$(\pm 0.1)^a$	$(\pm 0.9)^a$	$(\pm 30.4)^a$
	1,800	2.1	4.6×10^2	1.8×10^4	0.5	3.9	14.2
		$(\pm 0.3)^a$	$(\pm 1.8 \times 10^2)^a$	$(\pm 0.8 \times 10^4)^a$	$(\pm 0.1)^b$	$(\pm 0.8)^b$	$(\pm 3.3)^b$
	2,450	1.7	1.8×10^2	1.1×10^4	0.5	4.3	13.4
		$(\pm 0.9)^b$	$(\pm 0.5 \times 10^2)^b$	$(\pm 0.4 \times 10^4)^b$	$(\pm 0.1)^b$	$(\pm 0.7)^b$	$(\pm 4.3)^b$
P. nigra	650	1.9	5.6×10^2	1.1×10^4	1.4	12.1	123.3
		$(\pm 0.7)^a$	$(\pm 3.3 \times 10^2)^a$	$(\pm 0.8 \times 10^4)^a$	$(\pm 0.3)^a$	$(\pm 5.7)^a$	$(\pm 55.3)^a$
	950	1.5	3.5×10^2	1.0×10^4	1.2	12.8	134.2
		$(\pm 0.5)^b$	$(\pm 0.7 \times 10^2)^b$	$(\pm 0.8 \times 10^4)^a$	$(\pm 0.3)^a$	$(\pm 4.8)^a$	$(\pm 81.8)^a$
Q. coccifera	300	0.5	–	–	0.4	2.8	142.6
		$(\pm 0.0)^b$			$(\pm 0.2)^a$	$(\pm 0.6)^a$	$(\pm 158.4)^a$
	650	4.2	–	–	0.3	2.1	67.7
		$(\pm 0.0)^a$			$(\pm 0.1)^b$	$(\pm 0.6)^b$	$(\pm 28.9)^a$
Q. ilex	300	1.3	–	–	0.7	7.8	1,938.9
		$(\pm 1.8)^a$			$(\pm 0.4)^a$	$(\pm 1.4)^a$	$(\pm 605.7)^a$
	650	0.5	–	–	0.3	4.7	603.4
		$(\pm 0.0)^a$			$(\pm 0.1)^b$	$(\pm 1.4)^b$	$(\pm 417.3)^b$

Letters "a–b" show significant differences ($p < 0.05$) of the parameters examined among stations of the same species; "a" corresponds to the highest and "b" to the lowest values

* In *Pinus* spp., flowers and inflorescences are microsporophylls and strobili, respectively

Table 8 Representation of Pinaceae and *Quercus* taxa on Mt Olympos, in terms of surface that they occupy (V) and airborne pollen that they contribute (P), and the corresponding P/V ratio values

Taxon	Airborne pollen (P)		Surface covered (V)				P/V ratio	
			Mountain (V_1)		Catchment area (V_2)			
	(grains m^{-3})	(%)	(ha)	(%)	(ha)	(%)	P/V_1	P/V_2
Pinaceae[a]	9,877	31.5	23,827.5	46.4	13,076.2	55.9	0.68	0.56
Quercus[b]	7,458	23.8	14,057.7	27.4	4,684.4	20.0	0.87	1.19
Pinaceae/*Quercus*	1.32		1.69		2.79			

For P/V values close to 1, taxa are fairly represented, for values well above or below 1, they are over- or under-represented, respectively, in the airborne pollen compared to their vegetation cover

[a] *P. heldreichii*, *P. nigra*, *Abies borisii-regis*

[b] *Q. cerris*, *Q. coccifera*, *Q. frainetto*, *Q. ilex*, *Q. petraea*, *Q. pubescens*

not find any significant trend with elevation within the range 300–2,100 m. In contrast, Jochner et al. (2012) reported decrease with elevation within the range 700–1,700 m, whereas Gehrig and Peeters (2000) reported no reduction up to 1,500 m, but clear decrease above this altitude. The latter authors also stated that "due to the complex topography of the Prealps and Alps, it is not possible to propose a general rule of pollen reduction with increasing altitude". Our study on Mt Olympos clearly shows a pollen reduction with increasing elevation for the locally growing lowland (or mainly lowland) taxa.

There are intriguing results in the pollen patterns detected, as is the contribution of pollen from

Cannabaceae and *Ambrosia*, although their representatives are not recorded in the local vegetation (Strid 1980). Regarding *Ambrosia* pollen, it was detected in the air of Mt Olympos, as it is also detected in the air of Thessaloniki (Damialis et al. 2007). Up to now, *A. artemisifolia* has been found in only one location in Greece: in Epirus province, in the western part of the country, far away from Mt Olympos (Bergmeier 2008). However, in the neighbouring Bulgaria, it has been found to expand at a high rate (Dimitrov and Tzonev 2002; Vladimirov et al. 2007). According to Tutin et al. (1976), *A. maritima* L. is the only *Ambrosia* representative, native in Greece, but it has not been found in the vicinity of Mt Olympos. Presence of *Ambrosia* pollen even at high altitudes and absence of any pollen pattern with elevation suggest a medium- or long-range transport to the mountain.

Regarding pollen production, variability in the amount of pollen has been reported for several taxa growing in different climatic zones (Khanduri and Sharma 2002a; Mondal and Mandal 1998), among which for *Quercus* species (Gómez-Casero et al. 2004; Jato et al. 2007), and can be of considerable magnitude, particulary in CO_2 enriched environments (Wayne et al. 2002; LaDeau and Clark 2006; Rogers et al. 2006). However, we did not find notable differences in the pollen-related reproductive attributes of the four species with elevation; in fact, we found none for the evergreen oaks. Sampling stations have an elevation difference of 1,400 m for *P. heldreichii*, 300 m for *P. nigra* and 350 m for the two Mediterranean evergreen oaks. It seems that the environmental conditions associated with an elevation difference of 300–400 m in the Mediterranean-vegetation zone, where these evergreen oaks occur, do not suffice to trigger modified responses with respect to the quantitative aspects of their reproductive output (pollen and flowers).

The lack of elevation-related pollen-production plasticity contrasts reports for differing performance of *Quercus* representatives including *Q. coccifera* and *Q. ilex*, in Spain, in different years (Gómez-Casero et al. 2004; Jato et al. 2007). It is possible that the climatic difference among the elevation-different stations on Mt Olympos is less pronounced than the yearly variability at the Spanish sites. An alternative and/or complementary explanation is that, although belonging to the same species, the Greek and Spanish populations of *Q. coccifera* and *Q. ilex* differ markedly in their genetic composition. This may be particularly true for *Q. ilex* as populations in Spain belong to subsp. *ballota* (syn. *Q. rotundifolia, Q. ballota*), whereas in Greece to subsp. *ilex*.

The size of the units sampled (inflorescences, flowers) did not have any effect on the reproductive output (flowers, pollen) in *Quercus* species; it only affected *Pinus* species. Regarding growth attributes, the effect of plant height seems more important than of trunk perimeter on pollen yield at the level of crown.

The four species produce comparable amounts of pollen, at all scales examined, although they differ significantly in a number of attributes: pollen and flower production per inflorescence are higher in the two *Pinus* species, but *Q. coccifera* produces more pollen per flower and more inflorescences per m^2 of crown surface than all species.

Pollen production has been estimated for several *Pinus* representatives. At the scale of strobilus, we found *P. nigra* producing slightly more pollen grains (1.8×10^6) than *P. heldreichii* (1.2×10^6); at this scale, pollen production is reported as being within the narrow range 1.5×10^3–1.6×10^3 for *P. sylvestris* (Erdtman 1943; Pohl 1937; Sarvas 1962), as varying between 2.4×10^5 and 2.8×10^5 for *P. pinaster* (Tormo Molina et al. 1996), between 5.8×10^5 and 7.6×10^5 for *Pinus roxburghii* (Sharma and Khanduri 2002), and as equal to 3.5×10^5 for the Mediterranean pine *P. brutia* (Maraidoni 2011). Comparing these values (or the respective ones at other scales), we can conclude that pollen production for both *P. heldreichii* and *P. nigra* from Mt Olympos lies at the upper end of the range recorded so far for the genus.

Quercus coccifera was found producing slightly more pollen per flower (1.5×10^4) than *Q. ilex* (9.0×10^3). Reported values of pollen production for *Quercus* species at this scale are within the range 1.9×10^4–1.3×10^6 (Erdtman 1943; Moore et al. 1991; Tormo Molina et al. 1996; Gómez-Casero et al. 2004). We found these two evergreen oaks producing similar amounts of pollen at higher scales like per crown surface unit and individual. In contrast, *Q. coccifera* individuals were found less productive than *Q. ilex* ones in Spanish populations (Gómez-Casero et al. 2004). In general, pollen-production values for the two Mediterranean evergreen *Quercus* species from Greece lie at the lower end of the range recorded so far for the genus.

Given the limited responsiveness of the four species to the different environmental conditions associated

with the elevation at which they were studied, their pollen production does not seem to be an appropriate indicator for monitoring environmental change. This holds particularly true for the two evergreen oaks. Gómez-Casero et al. (2004) suggested that deciduous (oak) species may be more sensitive to changes in meteorological conditions than evergreen ones. Plant conservatism regarding pollen production has been previously reported and interpreted as resulting from the tendency to confine the amount of pollen produced within rather fixed margins; so, when one parameter, such as the number of pollen grains per flower, increases, another, such as the number of flowers per inflorescence, may decrease in compensation (Tormo Molina et al. 1996; Gómez-Casero et al. 2004).

The similarity in the amount of pollen produced by the *Pinus* and *Quercus* species studied and the higher concentration of airborne Pinaceae pollen in the mountainous area suggest a larger participation of Pinaceae as compared to *Quercus* in the vegetation of Mt Olympos. This is indeed the case. However, the Pinaceae to *Quercus* airborne pollen ratio is lower than the ratio of the surfaces that they cover. Assuming (1) that densities of Pinaceae and *Quercus* representatives are similar in areas of equal cover, and (2) that pollen produced by the other species of the same taxon is not overwhelmingly different to that estimated for the species that we studied, we can argue that airborne pollen does not depict accurately the participation of Pinaceae and *Quercus* in the local vegetation. In order to have an estimate whether Pinaceae are under-represented or *Quercus* over-represented, we made use of the *P/V* ratio that is commonly used in soil palynological studies (Heim 1970). Values of this ratio show that whereas *Quercus* species are fairly represented in the airborne pollen, Pinaceae are clearly under-represented.

It is well known that most of the released pollen is deposited close to its source, but a small fraction is uplifted above the canopy and then transported via horizontal winds far from its source. How far pollen particles move depends on many factors, including the rate at which they descend in still air owing to gravitational effects; dispersal distance and deposition rate are inversely related (Williams 2008). Pollen can be washed downward by heavy precipitation, re-suspended after drying and re-released for further aerial transport (Williams 2008). *Quercus* pollen morphology appears not to facilitate transport (Mandrioli et al. 1984) far from the source, in contrast to

Pinaceae pollen that can fly over long distances (Williams 2008; references therein); in fact, it is found that pine pollen is transported as far as 47–60 km within 3 h (Di-Giovanni and Kevan 1991). On Mt Olympos, *Quercus* taxa seem to be rather fairly represented in the airborne pollen, whereas Pinaceae taxa to be under-represented, in accordance with what would be expected on the basis of the morphological features of their pollen. These results also imply that a considerable part of Pinaceae pollen from Mt Olympos is transported and deposited elsewhere.

On the basis of the decreasing trends between elevation and pollen concentration in the air for the lowland taxa, we can argue that, within a margin of error, airborne pollen reflects pollen taxa distribution along the elevation gradient. This means that local pollen emissions play the major role in determining pollen season and abundance patterns. Nevertheless, there is evidence that medium or long-range transport does occur. Although an *Ambrosia*-free mountain, Mt Olympos is not equally *Ambrosia* pollen free. Plants producing it are not reported as occurring on the mountain or in its vicinity, but their pollen is detected at all altitudes. In consequence, Mt Olympos visitors cannot escape this highly allergenic pollen.

5 Conclusions

Airborne pollen in Mt Olympos National Park is dominated by Pinaceae and *Quercus* grains. Although there is no evidence of *Ambrosia*'s presence locally, its pollen is present from the foot up to very high altitudes. There are several pronounced changes of pollen-related features with elevation: the number of taxa substantially contributing pollen decreases by approximately 4 for every 1,000 m of elevation increase, whereas the average duration of the species' pollen seasons decreases by 3 days for every 100 m of elevation increase or by 5 days for every Celsius-degree of temperature decrease. Pollen production values for the Mediterranean evergreen *Q. coccifera* and *Q. ilex* lie at the lower end of those reported till now for the genus, whereas for the montane pines, *P. nigra* and *P. heldreichii*, they lie at the higher end. For all species, and primarily for the two *Quercus* species, pollen production does not seem to be an appropriate indicator of environmental change, as the two species appear quite conservative regarding this

attribute. The under-representation of pollen from Pinaceae in the total airborne pollen suggests its transport and deposition away from the mountain.

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